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Assessing the aggregated risk of invasive crayfish and climate change to freshwater crabs: A Southeast Asian case study

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ABSTRACT

Primary freshwater crabs represent a culturally and ecologically significant component of freshwater habitats globally that has a high percentage of threatened species. Invasive species (especially non-indigenous crayfish) and climate change are not only important standalone threats, but are also expected to compound existing threats (e.g., habitat loss/modification, pollution) and challenge the long-term survival of these decapod crustaceans. This study illustrates the importance of considering these two emerging and growing threats in conservation or management strategies by quantifying (via species distribution models) the individual and aggregated risks of these threats in Southeast Asia, a region with the highest diversity of primary freshwater crabs and a high proportion of imperiled species. Results predicted that most species of crabs (82.1%) will co-occur (and hence interact) with invasive crayfish to a moderate to high degree, and most species (69.2%) will also experience a reduction in suitable climate conditions in the future. In terms of aggregated risk, the results also predict an increased overlap between invasive crayfish and native crabs for three out of the seven species analyzed (namely *Procambarus virginalis*, *Cherax destructor* and *Orconectes rusticus*). Findings from this study provide a quantitatively derived rationale for the development of adaptive regulations and conservation plans in the region to minimize the risk of invasive species in a cost-effective way, thereby enabling the protection of Southeast Asia's natural heritage and its vital ecosystem services.

1. Introduction

Primary freshwater crabs represent a significant yet often understudied component of aquatic biodiversity that is particularly at risk to global change (Collen et al., 2014; Cumberlidge et al., 2009; Yeo et al., 2014). With over 1300 species described to date, this diverse group of brachyuran crabs (belonging to the families Gecarcinucidae, Potamidae, Potamonautidae, Pseudothelphusidae and Trichodactylidae) is largely circum-tropically distributed (Cumberlidge et al., 2009; Tsang et al., 2014; Yeo et al., 2008). They complete their entire lifecycle independent of a marine phase (Cumberlidge & Ng, 2009; Yeo et al., 2008), and play prominent ecological and cultural roles within their native range (Cumberlidge et al., 2009; Dobson et al., 2007; Yeo et al., 2008). Their ability to feed across multiple trophic levels makes them vital to the maintenance of the local food web assemblages (Dobson et al., 2007; Dudgeon & Cheung, 1990; Kasai & Naruse, 2003; Maitland, 2003), and their burrowing capabilities enables regulation of water levels in habitats (Dobson, 2004; Ng, 1989; Stahl et al., 2014). The cultural importance of freshwater crabs is reflected in their widespread consumption by with local groups in Asia and South America for food and medicinal purposes (Dai, 1999; Finkers, 1986; Ng, 1988; Yeo & Ng, 1998; Yeo et al., 2008).

Despite their significance, research efforts towards these decapods have been severely lacking (Cumberlidge et al., 2009). As a result, almost 50% of the freshwater crab species assessed in the 2008 International Union for Conservation of Nature (IUCN) Red List of threatened species were found to be data deficient (e.g., lacking sufficient population or distribution data) for determination of extinction risk (Cumberlidge et al., 2009). Existing threats to these crabs, however, are notable. Among the species with sufficient data for assessment, a relatively large proportion (34.8%) of freshwater crabs are near threatened or threatened (Cumberlidge et al., 2009). This level stems from both high levels of species endemism, as well as habitat change and pollution (Cumberlidge et al., 2009; Esser & Cumberlidge, 2008a; Esser & Cumberlidge, 2008b; Ng & Yeo, 2007). Specifically, agriculture and deforestation have been implicated as threats for a large number of threatened freshwater crab species in parts of Southeast Asia and Sri Lanka (Bahir, Ng, Crandall, & Pethiyagoda, 2005; Cumberlidge et al., 2009; Ng & Yeo, 2007; Pethiyagoda, 1994). As few conservation plans or efforts exist to safeguard threatened populations (Cumberlidge et al.,

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2009; Ng et al., 2014; Yeo et al., 2016), many species could face extinction in the near future, especially in light of their vulnerability to invasive species and climate change (Cumberlidge et al., 2009).

Biological invasions are known to have extensive ecological impacts especially within fresh waters (Beisel, 2001; Lodge et al., 1998). These impacts are typically pronounced for species such as freshwater crabs owing to their limited distribution (Cumberlidge et al., 2009; Ogada, 2006). One group of invaders that poses a notable threat to freshwater crabs is the non-indigenous crayfish species (NICS) (Foster & Harper, 2007; Ogada, 2006; Savvides et al., 2015). These mostly temperate decapod species, similar to freshwater crabs, complete their entire lifecycle in fresh waters, and affect habitats through their feeding and burrowing behavior (Crandall & Buhay, 2008; Larson & Olden, 2010; Reynolds et al., 2013). As a result, crayfish have a tendency to co-occur and directly interact with native crabs when released into tropical regions—an event that has received scientific attention, but is increasing in frequency and likelihood (Ahyong & Yeo, 2007; Hobbs et al., 1989; Lodge et al., 2012). For instance, the North American red swamp crayfish *Procambarus clarkii* has been shown to agonistically interact with and outcompete native freshwater crabs (Ogada, 2006; Savvides et al., 2015), with its competitive superiority linked to the decline of native crab populations following their invasion of rivers in Western Kenya (Cumberlidge et al., 2009; Foster & Harper, 2007; Ogada, 2006).

Such negative impacts are also likely to be affected by climate change. While human-induced climate change is forecast to cause alterations to ecosystem processes and increases in prevalence of human diseases (Sala et al., 2000; Thomas et al., 2004), many studies also predict its ability to cause biodiversity loss (Alamgir et al., 2015; IPCC, 2013; Poesch et al., 2016; Thomas et al., 2004). Species such as freshwater crabs (Cumberlidge et al., 2009; Woodward et al., 2010) are expected to face reductions in suitable habitat conditions (e.g., (Alamgir et al., 2015; Poesch et al., 2016)), and magnifications of other threats (Hellmann et al., 2008). For example, the vulnerability of native decapods in Europe to invasive impacts can be intensified because of the future range shifts and expansion of NICS (Capinha et al., 2013).

The combined threat of climate change and invasive species is of particular concern in Southeast Asia where 11 nations hold 20–25% of the world's native plant and animal biodiversity in roughly 4% of its land area (Sodhi et al., 2004; Woodruff, 2010). This region, with its rapidly growing human populations and economies, is already experiencing impacts associated with the growing number of invasive species (Nghiem et al., 2013). Specifically, the increasing introduction and establishment of NICS in the region (e.g., (Ahyong & Yeo, 2007; Patoka et al., 2016; Wanjit & Chaichana, 2013)) puts many freshwater crab species at risk (Lodge et al., 2012). This is likely to be further compounded by the effects of climate change that are predicted to cause losses of coastal systems, increased temperatures (up to 6 °C), and potentially drastic changes in climatic patterns in Southeast Asia (IPCC, 2007; IPCC, 2013). These emerging threats, together with the high levels of endemism and species richness of freshwater crabs (containing 30% of all extant species), mean that this region represents an important target for conservation research efforts (Cumberlidge et al., 2009; Yeo et al., 2016).

Consequently, this study focuses on Southeast Asian freshwater crabs, with the aim of assessing the aggregated risk of these two emerging and understudied threats. Here we quantify the vulnerability of freshwater crabs, through the use of species distribution modeling (SDM) of the seven most high-risk NICS and all native freshwater crabs in the region (under both current and future climate scenarios), to: 1) the (Grinnellian niche) overlap and co-occurrence with NICS; 2) projected future climate conditions (and their effects on availability of suitable habitat); and 3) shifts in risk of overlap resulting from climate change.

2. Methods

2.1. Study area, focal species and occurrence data

This study focused on countries in Southeast Asia (11°S–28°N and 92–141°E), a tropical region characterized by a warm and humid climate with monsoon seasonality (e.g., (Choi et al., 2009; Chotamonsak et al., 2011)). While the region is known to have a high number of endemic freshwater crabs (Cumberlidge et al., 2009; Yeo et al., 2008), Southeast Asia has almost no native crayfish (apart from Indonesian West Papua, part of the Australasian biogeographical region) (e.g., (Lukhaup, 2015)). However, NICS have been recorded from multiple locations within Southeast Asia, including Singapore (Belle et al., 2011), Malaysia (Awangku et al., 2016), Indonesia (Patoka et al., 2016), and Thailand (Wanjit & Chaichana, 2013), with unconfirmed reports from Philippines (Cagauan, 2007; Hentonnen & Huner, 1999).

This study focuses on seven NICS in two families as focal species—*Cherax destructor* and *C. quadricarinatus* (Parastacidae), and *Orconectes immunis*, *O. rusticus*, *O. virilis*, *Procambarus clarkii* and *P. virginalis* [Marmorkrebs] (Cambaridae). Although not all seven species have established populations within Southeast Asia, they represent those that are commonly traded internationally for food and as ornamental species (Chucholl & Wendler, 2017; Lodge et al., 2012; Zeng et al., 2015). They have long histories of introduction (Zeng et al., 2015), possess established populations within tropical, subtropical and temperate climates (e.g., (Feria & Faulkes, 2011; Zeng et al., 2016)), and have known negative impacts on recipient ecosystems (e.g., (Gherardi, 2007; Lodge et al., 2012)). Although a recent update of crayfish taxonomy classifies all three *Orconectes* species under the genus *Faxonius* (Crandall & De Grave, 2017), this study retains the use of *Orconectes*, which is widely used in invasion biology literature (e.g., (Larson et al., 2017)). Locality information for these crayfishes was gathered from a variety of sources including recent sampling efforts within the region (Singapore and Malaysia), museum records (e.g., Lee Kong Chian Natural History Museum, Singapore; Smithsonian National Museum of Natural History, USA), online databases (e.g., Global Biodiversity Information Facility (http://www.gbif.org); The IUCN Red List of Threatened Species (http://www.iucnredlist.org)), and published literature (e.g., (Feria & Faulkes, 2011; Kawai et al., 2009; Zeng et al., 2016)) (Appendix S1).

The location data for all 396 species of freshwater crabs within Southeast Asia (as of 2012; (Freitag, 2012; Yeo et al., 2008)) was also gathered from similar data sources—recent sampling efforts, museum records, onlxine databases, and published literature (Appendix S1). Localities of these crab species (which belong to the families Potamidae and Gecarcinucidae) were then plotted onto the map of Southeast Asia, at a resolution of 2.5 arc min (~25 km^2), and duplicates within each cell were removed. Crab species with more than four occurrence points were selected for SDMs (n = 39).

2.2. Forming SDMs, and projecting current and future climate scenarios

This study used Maxent (version 3.3.3 k) to model species distributions (Phillips et al., 2006) because of its ability to handle presence-only data and small sample sizes (n = 4–7), while producing highly accurate predictions (Hernandez et al., 2006; Rhoden et al., 2017; Wisz et al., 2008). Set within a machine-learning framework, Maxent allows users to project a species' likely distribution over temporal and spatial scales based on the relationship between environmental variables and locality information (Phillips et al., 2006). It also allows for adjustments within the tool, catering to species-specific situations, and improving the accuracy of SDMs (see (Muscarella et al., 2014)).

While only the native range of crabs was considered during SDM formation (to approximate the native realized Grinnellian niche), the full range (both native and alien) of each crayfish species was used to

approximate its fundamental niche (Capinha et al., 2011; Rodda et al., 2011; Soberón, 2007; Zeng et al., 2016). The latter served to improve the "transferability" of SDMs, and reduce the effects of niche shift associated with alien species (Capinha et al., 2011; Zeng et al., 2016). Pseudo-absences (maximum of 10,000; (Phillips, 2008)) were selected from an extent of 250-arc-minutes around each locality (Barve et al., 2011; Zeng et al., 2016), and using a bias file that indicated the correlation between accessibility and sampling (Fourcade et al., 2014; Uchida & Nelson, 2009). A total of 24 environmental variables was considered, including 19 bioclimatic variables from WorldClim (Hijmans et al., 2005), breakline emphasis (be_grd) from Digital Elevation Model GMTED 2010 (Danielson & Gesch, 2011), flow accumulation (flow_accumu), conditional digital elevation models (cond dem), as well as aspect and slope (derived), from USGS HydroSHEDS (http://hydrosheds.cr.usgs.gov).

A stepwise reduction of collinear variables (evaluated via variance inflation factor (VIF)) was then used to account for multicollinearity, limiting the final dataset to VIF values < 10 (Merow et al., 2013). An additional series of stepwise variable removal was then used to reduce any potential noise to the SDMs that could have arisen from extraneous variables (following (Zeng et al., 2016)). Within this process, each iteration of the stepwise removal was tuned with beta regularization coefficients ranging from 0.5 to 8 with increments of 0.5, and the feature classes—"L", "LQ", "LQH", "LQHP", "LQHPT" (L: linear; Q: quadratic; H: hinge; P: product; T: threshold; following (Merow et al., 2013; Muscarella et al., 2014)). Model performances were evaluated via the mean Area Under Curve of receiver operating characteristic curve (AUC) based on the testing data. These testing datasets were created via partitioning of both presence and pseudo-absence points. Freshwater crab data were partitioned via the jackknife method (owing to the small sample sizes; following (Hernandez et al., 2006; Pearson et al., 2007; Shcheglovitova & Anderson, 2013)); the NICS dataset was partitioned via the block method (four data groups following the division along longitude and latitudes), enabling more accurate extrapolation of SDMs (Muscarella et al., 2014; Wenger & Olden, 2012).

The most optimum and accurate SDM of each species was then used for projection onto current environmental datasets within Southeast Asia. Crayfish distributions were projected onto the entire region (indicating vulnerability to NICS establishment), while crab distributions were constrained to their occurring drainages (HydroSHEDS: http://hydrosheds.cr.usgs.gov), given their relatively poor dispersal ability beyond natural watersheds (France, 1992; Yeo et al., 2008). This process was then repeated, and projected based on future climate environmental variables obtained by downscaling global climate models (GCMs) that reflect four Representative Concentration Pathways (RCPs) scenarios indicating different radiative forcing values (RCP2.6, RCP4.5, RCP6.0, RCP8.5) for the years 2050 and 2070 (Hijmans et al., 2005). The GCMs used in this study were derived from the Beijing Climate Center Climate System Model (BCC_CSM1.1), Community Climate System Model version 4 (CCSM4), and Hadley Global Environment Model 2-Atmosphere (HadGEM2-AO). This process was bootstrapped 10 times for each species and averaged across each climate scenario and year, producing nine predicted distributions (one current and eight future) for each of the 39 freshwater crab species and seven NICS.

2.3. Evaluating risk of NICS and climate change to freshwater crabs

Individual projections under current climate conditions were stacked to visualize the diversity of freshwater crabs as well as the collective establishment risk of NICS to Southeast Asia. To quantify the relative risk of co-occurrence (and hence interaction) each NICS poses to the freshwater crab species, we then calculated the Schoener's D between all the NICS-crab species pairs (Schoener, 1968; Warren et al., 2010). This index measures the degree of niche (and distribution) overlap, with values ranging from 0 to 1, and larger values indicating greater overlap (Rödder & Engler, 2011; Schoener, 1968). These calculated values were illustrated with a heatmap to indicate the degree of risk associated with each NICS, and corresponding vulnerability of each crab species. Species exhibiting similar risk and vulnerability were clustered together (Euclidean).

Changes to habitat suitability resulting from climate change were then mapped using the differences between stacked projections formed under future climate scenarios and current conditions. Impacts of climate change on individual species of freshwater crabs were quantified by calculating the differences in each species' projections (between current and future conditions). The differences within known species localities were then extracted to determine the effect of climate change on the individual crab species. Habitat suitability scores range from −1 to 1, with negative values indicating a decrease in suitability.

These projections were then used to determine the degree of niche overlap (Schoener's D) under the various future climate scenarios, and visualized using heatmaps. The effects of climate change on this risk of overlap was summarized for each NICS by calculating the overall differences in Schoener's D across all freshwater crabs. Negative values from the differences denote a decrease in the degree of niche/distribution overlap, while positive indicates an increase.

All analyses were performed on R version 3.0.2 (R Development Core Team, 2013), with model formation and evaluation, and quantification of overlap performed using the package "ENMeval" (Muscarella et al., 2014). While stepwise exclusion of collinear variables was performed via the package "usdm" (Naimi, 2015). An example of analysis is provided in Appendix S2.

3. Results

3.1. Species localities, model optimization and projections

Species occurrence data for freshwater crabs (758 localities) indicated continuous distribution around Southeast Asia, with higher species densities within Peninsular Malaysia and Thailand (Fig. 1). A large number of the 396 species of freshwater crabs are highly stenotopic or only known from the type locality (Cumberlidge et al., 2009), resulting in a substantial reduction in species with five or more localities ($n = 39$). Within Southeast Asia, established populations of NICS were recorded from parts of Indonesia, Malaysia, Singapore and Thailand (Fig. 1), with *C. quadricarinatus* accounting for the majority (40 localities), and *P. clarkii* reported from two localities in Thailand (Wanjit & Chaichana, 2013).

The construction of 800–960 individual tuning models per freshwater crab species and NICS, revealed that the most accurate models of each species had a generally high predictive accuracy for both freshwater crabs (AUC_{Train}: 0.914 ± 0.103; AUC_{Test}: 0.843 ± 0.114; see Appendix S1) and NICS (AUC_{Train}: 0.793 ± 0.046; AUC_{Test}: 0.753 ± 0.065; see Appendix S1). These models also had a low degree of overfitting for freshwater crabs (AUC_{Diff}: 0.102 ± 0.072; see Appendix S1) and NICS (AUC_{Diff}: 0.079 ± 0.044; see Appendix S1).

The compiled (stacked) projections of these SDMs showed that under current climate conditions, parts of Myanmar, Thailand and Laos are able to support a high diversity of freshwater crabs (Fig. 2), while other parts of Indochina (especially major river systems of the Irrawaddy, Chao Phraya and Mekong) have relatively less high freshwater crab species diversity but have the potential to support more NICS (Fig. 3).

3.2. Risk of overlap between freshwater crabs and NICS

The parallel between the projected diversity patterns of both crabs and crayfish is also reflected in overall similarity between the Grinnellian niche of most (six of the seven) NICS and crabs assessed (Fig. 4). With the exception of *O. rusticus* (OcR) (Schoener's D < 0.15), most NICS indicated moderate to high degrees of overlap with most crab species, and *C. quadricarinatus* (ChQ), *P. virginalis* (PcV), *P. clarkii*

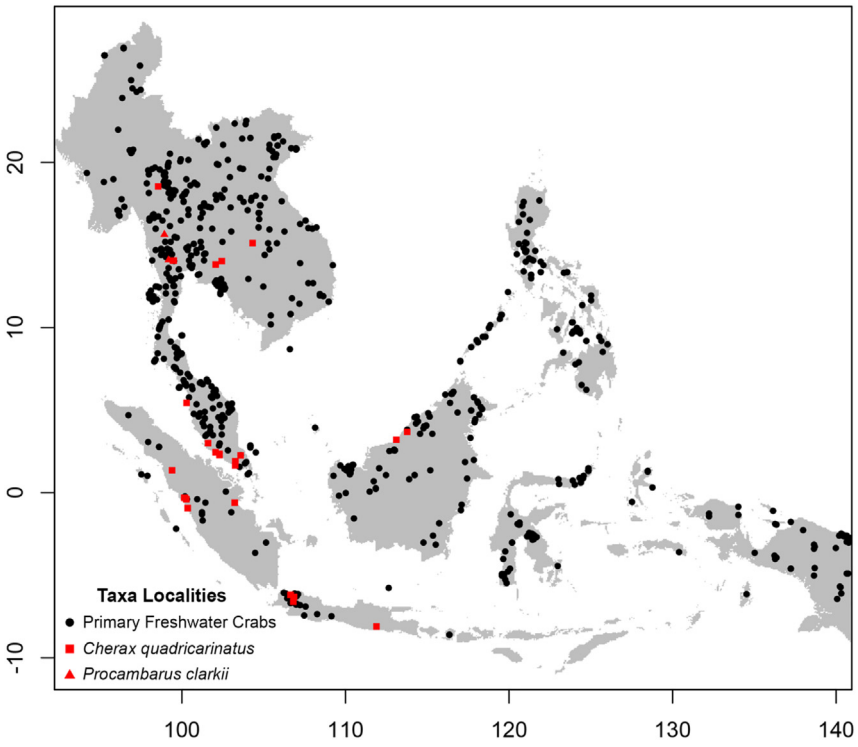

Fig. 1. Known point localities within SEA of primary freshwater crab species populations (black circles), and established populations of two NICS species—*Cherax quadricarinatus* (red squares) and *Procambarus clarkii* (red triangles). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(PcC), and *C. destructor* (ChD) forming a distinct high-risk cluster (Fig. 4; Appendix S1). In contrast, only seven species of freshwater crabs are of low vulnerability to NICS, while the majority (82.1%) of crab species are predicted to be of moderate to high vulnerability (Fig. 4; Appendix S1).

3.3. Climate change effects—habitat suitability changes for freshwater crabs

In addition, many freshwater crab species also appear to be negatively affected by future climate scenarios (Fig. 2; Appendix S1, S3). Projections formed under RCP2.6 (2050) indicate a mild decrease in habitat suitability in parts of Malaysia, Indonesia and Myanmar, while supporting a greater diversity of freshwater crabs in parts of Indochina (Fig. 2). However, by 2070 the predicted climatic conditions (RCP2.6) would generally support less diversity, with a larger portion of Indochina showing a decrease in habitat suitability (Fig. 2). Under scenarios for higher radiative forcing target levels, such changes would be more pronounced (see Appendix S3 for RCP4.5 and RCP6.0), with RCP8.5 (2050 and 2070) indicating the prominent differences (Fig. 2). This projected decrease in freshwater crab diversity across all scenarios is likely attributed to the negative habitat suitability scores associated with 27 of the 39 species (Fig. 5). Although climate change might have no clear impact on some species (e.g., *Siamthelphusa acutidens*) and even benefit others by increasing habitat suitability within known area of

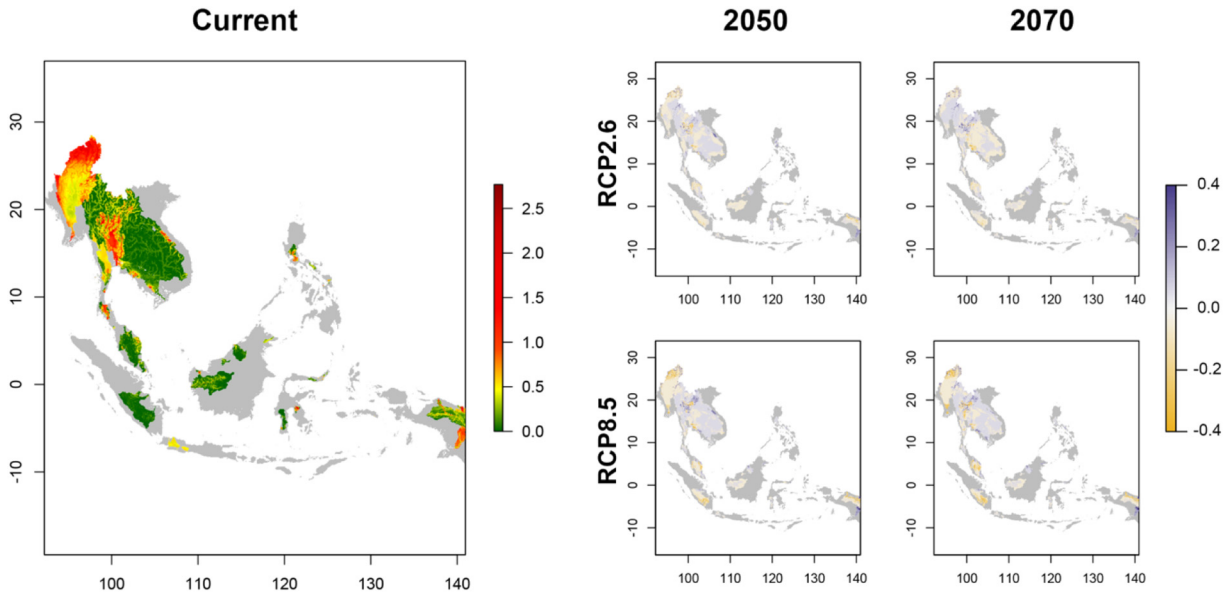

Fig. 2. Stacked-SDMs of 39 species of primary freshwater crabs (those with 5 or more occurrence points) within SEA formed under current climate conditions (left). Differences in diversity patterns between future and current climate conditions were also projected based on the scenarios RCP2.6 and RCP8.5, and years 2050 and 2070.

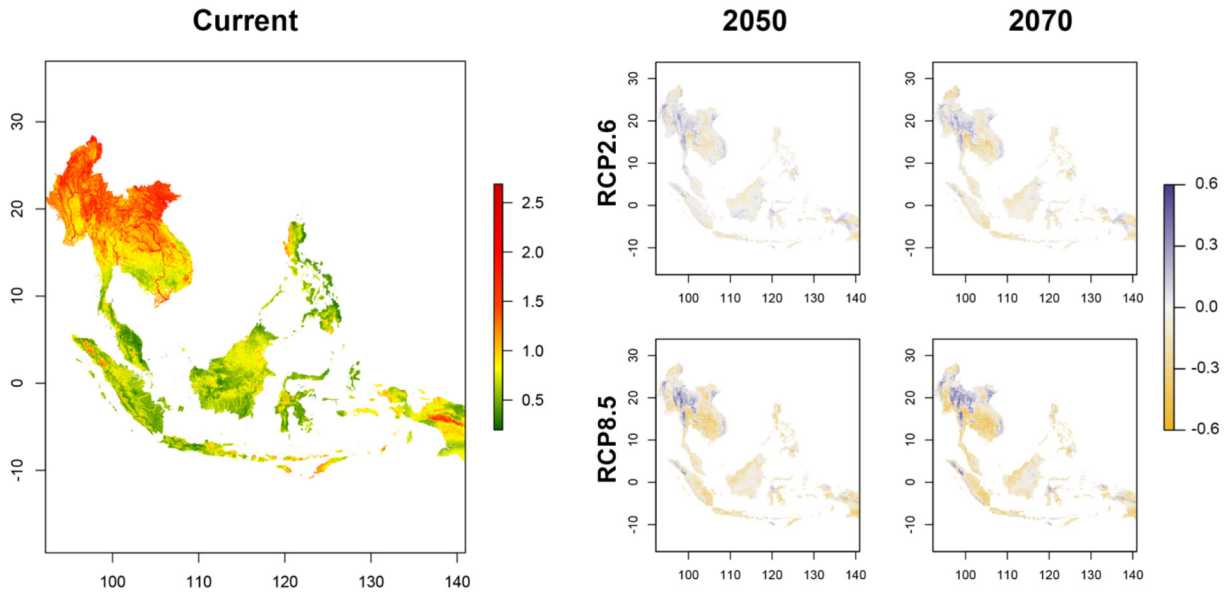

Fig. 3. Stacked-SDMs representing the potential distribution of NICS within SEA formed under current climate conditions (left). Differences in potential diversity patterns between future and current climate conditions were also projected based on the scenarios RCP2.6 and RCP8.5, and years 2050 and 2070.

occurrences (e.g., *Eosamon boonyaratae*), the majority of species (69.2%) are predicted to experience a reduction in suitable habitats as a result of climate change (Fig. 5).

3.4. Shifting risk of NICS from climate change

Climate change is also likely to affect NICS to varying degrees. The scenario RCP2.6 indicates changes in distribution patterns, with habitat suitability increasing in parts of Indochina, Peninsular Malaysia, Borneo and West Papua, while decreasing in other areas. This change is more pronounced in 2070 when compared to 2050, with higher RCP scenarios and later years giving rise to larger changes in habitat suitability (Fig. 3; Appendix S1, S3). This shift in the potential for habitats to support varying levels of diversity of NICS is reflected in the changes to predicted niche overlap patterns (Appendix S4). This results in a general reduction of the number of crab species in the low vulnerability cluster, while increasing the number of species in the high vulnerability cluster in some scenarios (e.g., RCP 2.6 in 2070) (Appendix S4). Some species in particular, would have a higher chance of overlap with freshwater crabs under the climate change scenarios, namely *P. virginalis*, *C. destructor* and *O. rusticus* (Fig. 6). These species show an increase in the overall Schoener's D values, while only *P. clarkii* has a predicted reduction in its degree of niche overlap (Fig. 6).

4. Discussion

Results from this study demonstrate that climate change and NICS pose notable threats to Southeast Asian freshwater crabs both individually as well as in tandem. NICS alone are expected to overlap and co-occur to a moderate or high degree with roughly 82% of the freshwater crabs, all climate change scenarios are projected to reduce the habitat suitability for about 69% of the crab species. Future climate scenarios are also expected to increase the risk of overlap with freshwater crabs for three of the seven NICS, while reducing the potential risk of only one crayfish species.

The SDMs constructed in this study (via an intensive tuning and variable optimization process) were predictive, but not overfitted, indicating a congruence between species localities and projections (Appendix S1). When the models constructed for the seven NICS were extrapolated onto the entire Southeast Asian region, they indicated a generally higher likelihood of establishment for *Cherax* and *Procambarus* species than *Orconectes* (Appendix S4). This is because species models of the former possessed response curves that match temperature and precipitation patterns of the region, unlike those of *Orconectes* species. For instance, the average temperature of the driest quarter (bio9) was among the most important variables identified for *O. virilis* and *O. rusticus*. Response curves of this variable indicate an increased likelihood of establishment at lower temperatures (< 20 °C) for both species—temperatures that correspond (and explains the restriction of *Orconectes* species) to temperate areas around Europe and North America (Olden et al., 2011; Rosenthal et al., 2006; Schrimpf et al., 2013). In comparison, *Cherax* and *Procambarus* species are more adapted to the tropical Southeast Asia climate, with the average temperature of the wettest quarter (bio8) identified as one of the most important predictors of *C. quadricarinatus* and *P. virginalis*. Low values of this variable are associated with low likelihood of establishment for both species, while temperatures of around 25–30 °C—conditions consistent with the climate of Southeast Asia (e.g., (Choi et al., 2009; Chotamonsak et al., 2011))—correspond with a drastic increase in establishment likelihood. Hence, considering the physiological importance of such temperatures for both survival and reproductive success (García-Guerrero et al., 2003; King, 1994; Meade et al., 2002; Seitz et al., 2005; Vogt, 2015), current models appear to reasonably and accurately explain and predict establishment risk. This also explains the discovery of > 20 distinct established populations of *C. quadricarinatus* and two of *P. clarkii* in Southeast Asia (Fig. 1) ((Awangku et al., 2016; Belle et al., 2011; Cagauan, 2007; Patoka et al., 2016; Wanjit & Chaichana, 2013); present study).

The existing established populations and collective potential distribution of these NICS therefore represent a conservation issue for Southeast Asia and its freshwater crabs. This is especially pertinent given the reported negative impacts of invasive crayfish on crop production (Acre & Diéguez-Uribeondo, 2015; Anastácio & Marques, 1996) and infrastructure (Acre & Diéguez-Uribeondo, 2015; Wizen et al., 2008) in a region where agriculture is of great economic importance (Gutiérrez & Reaser, 2005; Nghiem et al., 2013; Sodhi et al., 2010). NICS also indicate a potential for moderate to high distribution and Grinnellian niche overlaps with many crab species (~82%; Fig. 4). While variation would exist between various species combinations (affected by factors such as phylogeny), this propensity for co-occurrence (and resultant interactions) nonetheless represents a notable threat to native crabs that could result in direct reduction in native

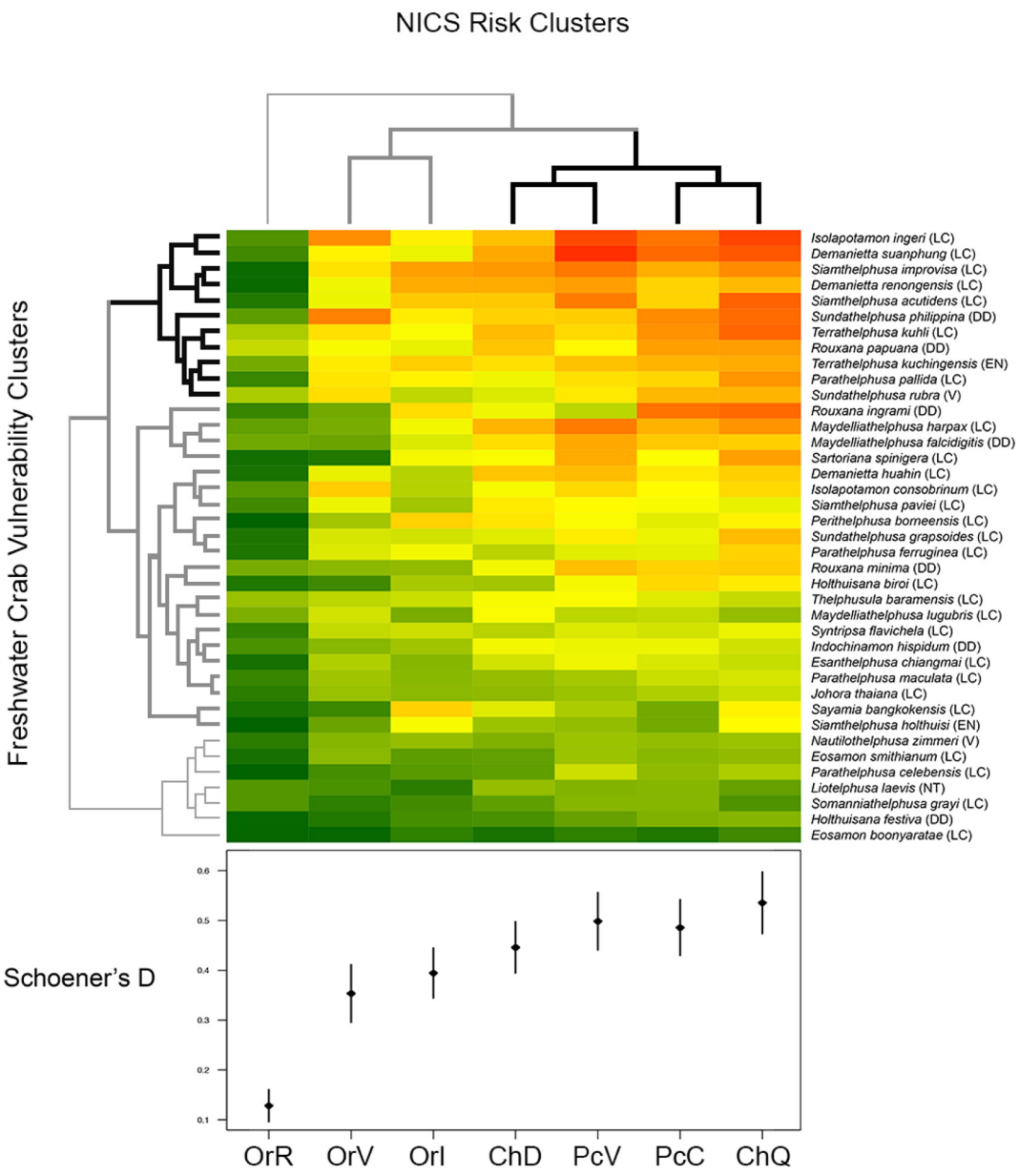

Fig. 4. Heatmap indicating the degree of niche overlap (Schoener's D) between multiple pairwise comparisons of NICS and freshwater crabs under current climate conditions. Risk clusters indicate NICS with similar likelihoods of niche overlap with primary freshwater crabs, while vulnerable clusters indicate freshwater crabs that are at risk from such overlap. Thickness and darkness of lines indicate risk/vulnerability clusters (thickest and darkest—high-risk; thinnest and lightest—low-risk). Increasing likelihood of co-occurrence via niche overlap is represented by a transition of colors from green (low Schoener's D) to yellow (moderate Schoener's D) and to red (high Schoener's D). Mean Schoener's D and the associated 95% confidence intervals are also indicated for NICS—*Cherax destructor* (ChD), *Cherax quadricarinatus* (ChQ), *Orconectes immunis* (OrI), *Orconectes rusticus* (OrR), *Orconectes virilis* (OrV), *Procambarus clarkii* (PcC) and *Procambarus virginalis* (PcV). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

populations. Mediated through their behavior and ecological interactions (Barbaresi & Gherardi, 1997; Gherardi & Cioni, 2004; Ogada, 2006; Pretzmann, 1987; Savvides et al., 2015), as well as disease and parasite transmissions (Avenant-Oldewage, 1993; Svoboda et al., 2014), NICS can directly impact native crabs (Foster & Harper, 2007; Ogada, 2006). These impacts are likely more pronounced for the high-risk species (e.g., *Procambarus* and *Cherax* spp.), considering the extent of overlap as well as their invasiveness and ability to impact native decapods (Beatty, 2006; Jones et al., 2009; Ogada, 2006; Zeng, 2017). Such impacts can spread to larger scales (e.g., watersheds) through the disruption of the important ecosystem services, making the control of NICS introduction a conservation priority (Cumberlidge et al., 2009; Ogada, 2006; Yeo et al., 2008).

The SDMs also indicate that many freshwater crab species will be directly affected by climate change. Up to 69% of freshwater crabs are likely to experience a reduction in habitat suitability regardless of future climate scenarios (Fig. 5), implying a constriction of optimal climatic niches by the year 2050. This would translate to greater pressure on the survival of these freshwater crabs (irrespective of their phylogeny), especially considering their limited dispersal ability and possible inability to shift their range or adapt to changing environmental conditions (Cumberlidge et al., 2009; Ng & Yeo, 2007; Yeo et al., 2008). For example, *Terrathelphusa kuchingensis* is expected to experience a 75% (mean) reduction of suitable climatic condition (Fig. 5). This can directly affect the species survival, while the ecology and changing land-use around the crab's habitat makes adaptations to such changes unlikely (Cumberlidge et al., 2009; Esser & Cumberlidge, 2008a).

In addition, climate change would further impact freshwater crabs

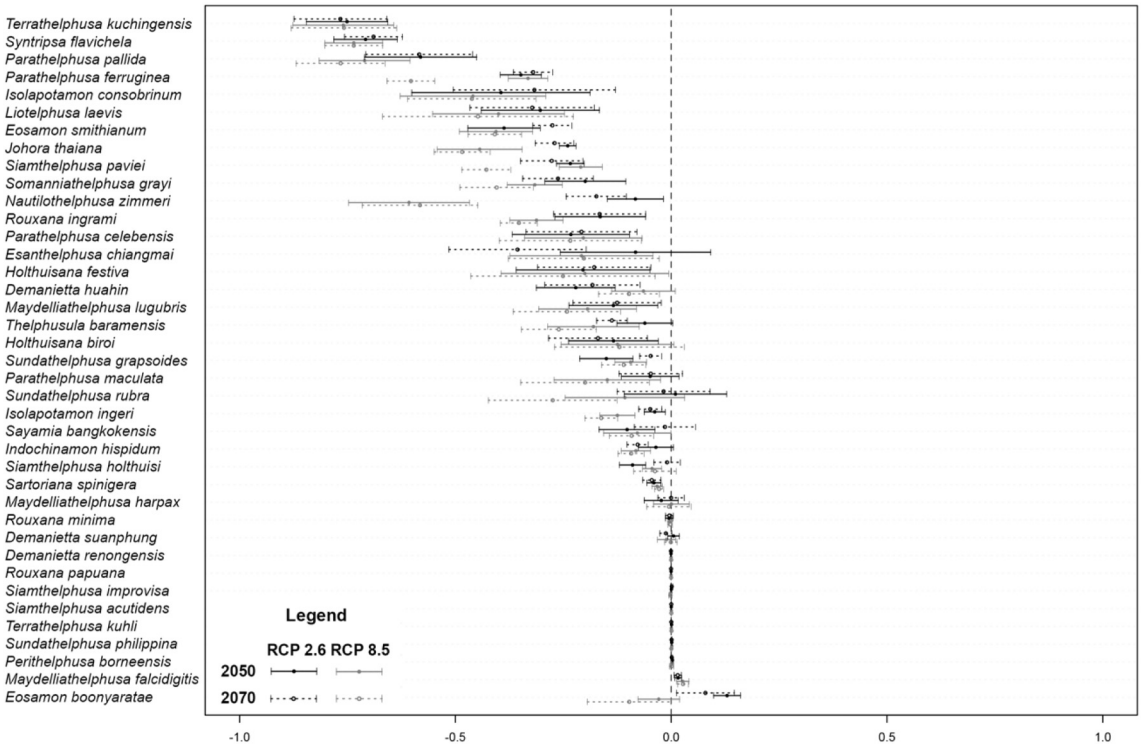

Fig. 5. Differences in habitat suitability between current climate conditions and future scenarios—RCP2.6 in 2050 (black closed circles) and 2070 (black open circles), as well as RCP8.5 in 2050 (gray closed circles) and 2070 (gray open circles)—for all 39 primary freshwater crab species. Error bars denote 95% confidence intervals. Species has been ranked from the largest reduction in habitat suitability (negative values) to largest increase in suitability (positive values).

through an increased risk of overlap with some NICS. Although *P. clarkii* shows a decrease in niche overlap, three other NICS are predicted to co-occur with more freshwater crab species in the future (Fig. 6). This increased risk of overlap corresponds to a greater number of vulnerable species (Appendix S4), and illustrates the potential for multiple threats to increase the extinction risk of freshwater crabs. Species such as *Sundathelphusa rubra*, which is already experiencing effects of habitat degradation (Esser & Cumberlidge, 2008b), will have fewer ideal habitats (with optimal abiotic conditions) as a result of reductions in habitat suitability (Fig. 5). Concurrently, the lowering of environmental barriers (due to climate change) to the establishment of NICS would increase the potential distribution of some species, corresponding to a greater risk of co-occurrence and interaction between the decapods (Appendix S4).

The combined threats are also likely to have pronounced effects on many of the stenotopic and endemic freshwater crab species. Although a number of freshwater crabs were not analyzed in this study due to their small range sizes, many species (n = 66) in Southeast Asia are already listed as threatened. Multiple threats, together with links between small range sizes and extinction risks (Giam et al., 2011; Purvis

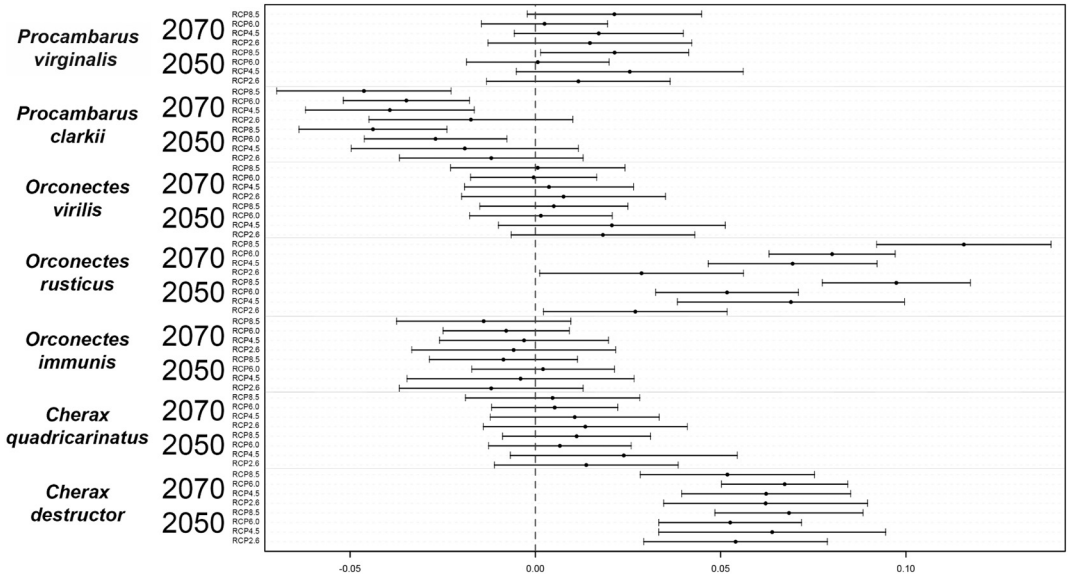

Fig. 6. Differences in the degree of niche overlap (of each NICS across all freshwater crab species) between climate conditions and future scenarios (RCP2.6, RCP4.5, RCP6.0, RCP8.5) for the years 2050 and 2070. Error bars denote 95% confidence intervals.

et al., 2010; Thomas et al., 2004), suggest that current predictions of species impacted by climate change and NICS are underestimates, highlighting the need for more conservation efforts in the near future.

To date, several steps have been taken towards the conservation of freshwater crabs (Cumberlidge et al., 2009; Ng et al., 2015; Yeo et al., 2016). The assessment of extinction risk for the IUCN Red List has enabled conservation via the provisioning of objectivity, credibility and political motivation (Bahir et al., 2005; Cumberlidge et al., 2009). This has translated in one case to an ongoing, concerted, multi-stakeholder effort directed towards the preservation of the Singapore freshwater crab, *Johora singaporensis* (Ng et al., 2015; Yeo et al., 2016). Should such endeavors be expanded to other species, rapid declines resulting from existing threats can be averted (Cumberlidge et al., 2009; Ng & Yeo, 2007; Sodhi et al., 2008). Yet results from this study underscore the importance of not just considering immediate threats, but also external and more long-term issues.

Although uncertainty (with regards to the mechanism and degree of interaction between specific species combinations) does exist within this study, it at least allows a conservative estimate/identification of both high- and low-risk NICS with respect to their potential threats to Southeast Asian freshwater crabs. This offers a quantitatively derived rationale for the development/alteration of regulations that could still allow the trade (and reap the associated economic and cultural benefits) of certain crayfish species, while mitigating the overall potential impact of other NICS on freshwater crabs; furthermore if decision/policy-makers consider complementary approaches such as trait-based risk assessments (e.g., (Zeng et al., 2015)) and added broader risk analyses that take into account impacts beyond those on freshwater crabs (e.g., macrophytes, fish, and amphibians), this could lead to development of more general policy/trade recommendations. This would serve as a more economically viable means of reducing such impacts (Leung et al., 2002; Lodge et al., 2016) that is especially relevant to Southeast Asia considering the history of species introductions promoted through agriculture and aquaculture trade (Gutiérrez & Reaser, 2005; Nghiem et al., 2013; Sodhi et al., 2010), often with little concern for the potential impacts on local ecosystems or communities (Gutiérrez & Reaser, 2005; Peh, 2010). Little regional legislation specifically addressing invasive species exists to date (Gutiérrez & Reaser, 2005; Peh, 2010); this is both a contributing factor to and a result of the dearth of impact or risk assessments of such species. This study therefore represents an important first attempt in addressing this gap, while balancing the conservation priorities directed towards freshwater crabs. It also allows for the adjustments of such conservation efforts to account for future changes in climatic conditions, enabling the development of adaptive conservation and management strategies. Specifically, results suggest the potential for future climate scenarios to lower the risk of *P. clarkii* co-occurring with native crabs (Fig. 6). Thus *P. clarkii* represents—at least based on SDM applied to tropical Southeast Asia—a potential alternative to *P. virginalis* for the aquarium or aquaculture trade (a “bonus” being that *P. clarkii* is already heavily traded). Such a strategy, however, may be complicated or even negated by other traits linked to the high specific invasive risk of *P. clarkii (Zeng et al., 2015)*. Here the results can also help by suggesting another possible replacement of *P. virginalis* in the aquarium and aquaculture trade, e.g., consistently low risk species (in Southeast Asia by SDM) such as *O. rusticus*.

5. Conclusions

These findings identify the vulnerability of certain freshwater crab species to both NICS and climate change, emphasizing the need to consider both threats in future conservation endeavors. It also exemplifies a technique that can form accurate predictions with limited data (only location information), and serve to guide adaptive conservation or management plans that reduce the likelihood for potential impacts in light of climate change, while permitting the realization of ecosystem services associated with non-indigenous species. Through such efforts, the preservation of these crabs would serve both to protect Southeast Asia's natural heritage, and maintain the ecosystem functioning of the region's freshwater habitats.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2018.04.033.

References

Acre, J.A., Diéguez-Uribeondo, J., 2015. Structural damage caused by the invasive crayfish *Procambarus clarkii* (Girard, 1852) in rice fields of the Iberian peninsula: a study case. Arch. Hydrobiol. 186, 259–269.
Ahyong, S.T., Yeo, D.C.J., 2007. Feral populations of the Australian red-claw crayfish (*Cherax quadricarinatus* von martens) in water supply catchments of Singapore. Biol. Invasions 9, 943–946.
Alamgir, M., Mukul, S.A., Turton, S.M., 2015. Modelling spatial distribution of critically endangered Asian elephant and Hoolock gibbon in Bangladesh forest ecosystems under a changing climate. Appl. Geogr. 60, 10–19.
Anastácio, P.M., Marques, J.C., 1996. Crayfish (*Procambarus clarkii*) effects on initial stages of rice growth in the Lower Mondego River valley, Portugal. In: Freshwater Crayfish. 11. pp. 608–618.
Avenant-Oldewage, A., 1993. Occurrence of *Temnocephala chaeropsis* on *Cherax tenuimanus* imported into South Africa, and notes on its infestation of an indigenous crab. S. Afr. J. Sci. 89, 427–428.
Awangku, S.N., Khairul, A.A.R., Shabdin, M.L., Faznur, F.F.N., 2016. The spread of the Australian redclaw crayfish (*Cherax quadricarinatus* von martens, 1868) in Malaysia. J. Sustain. Sci. Manag. 11, 31–38.
Bahir, M.M., Ng, P.K.L., Crandall, K., Pethiyagoda, R., 2005. A conservation assessment of the freshwater crabs of Sri Lanka. Raffles Bull. Zool. (Suppl. 12), 121–126.
Barbaresi, S., Gherardi, F., 1997. Italian freshwater decapods: exclusion between the crayfish *Austropotamobius pallipes* (Faxon) and the crab *Potamon fluviatile* (Herbst). Bull. Fr. Peche Piscic. (347), 731–747.
Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S.P., Peterson, A.T., Soberón, J., Villalobos, F., 2011. The crucial role of the accessible area in ecological niche modelling and species distribution modelling. Ecol. Model. 222, 1810–1819.
Beatty, S., 2006. Translocations of Freshwater Crayfish: Contributions from Life Histories, Trophic Relations, and Diseases of three Species in Western Australia (Ph.D. Thesis). Murdoch University, Perth.
Beisel, J.-N., 2001. The elusive model of a biological invasion process: time to take differences among aquatic and terrestrial ecosystems into account? Ethol. Ecol. Evol. 13, 193–195.
Belle, C.C., Wong, J.Q.H., Yeo, D.C.J., Tan, S.H., Tan, H.H., Todd, P.A., 2011. Ornamental trade as a pathway for Australian redclaw crayfish introduction and establishment. Aquat. Biol. 12, 69–79.
Cagauan, A.G., 2007. Exotic aquatic species introduction in the Philippines for aquaculture: a threat to biodiversity or a boon to the economy? J. Environ. Sci. Manag. 10, 48–62.
Capinha, C., Leung, B., Anastácio, P., 2011. Predicting worldwide invasiveness for four major problematic decapods: an evaluation of using different calibration sets. Ecography 24, 448–459.
Capinha, C., Larson, E.R., Tricarico, E., Olden, J.D., Gherardi, F., 2013. Effects of climate change, invasive species, and disease on the distribution of native European crayfishes. Conserv. Biol. 27, 731–740.
Choi, G., Collins, D., Ren, G., Trewin, B., Baldi, M., Fukuda, Y., ... Zhou, Y., 2009. Changes in means and extreme events of temperature and precipitation in the Asia-Pacific Network region, 1955–2007. Int. J. Climatol. 29, 1906–1925.
Chotamonsak, C., Salathé Jr., E.P., Kreasuwan, J., Chantara, S., Siriwitayakom, K., 2011. Projected climate change over Southeast Asia simulated using a WRF regional climate model. Atmos. Sci. Lett. 12, 213–219.
Chucholl, C., Wendler, F., 2017. Positive selection of beautiful invaders: long-term persistence and bio-invasion risk of freshwater crayfish in the pet trade. Biol. Invasions 19, 197–208.
Collen, C., Whitton, F., Dyer, E.E., Baillie, J.E.M., Cumberlidge, N., Darwall, W.R.T., ... Böhm, M., 2014. Global patterns of freshwater species diversity, threat and endemism. Glob. Ecol. Biogeogr. 23, 40–51.
Crandall, K.A., Buhay, J.E., 2008. Global diversity of crayfish (Astacidae, Cambaridae,

and Parastacidae—Decapoda) in freshwater. In: Balian, E.V., Lévequè, C., Segers, H., Martens, M. (Eds.), Freshwater Animal Diversity Assessment. Hydrobiologia. 595. pp. 295–301.
Crandall, K.A., De Grave, S., 2017. An updated classification of the freshwater crayfishes (Decapoda: Astacidea) of the world, with a complete species list. The. J. Crustac. Biol. 37, 615–653.
Cumberlidge, N., Ng, P.K.L., 2009. Systematics, evolution and biogeography of freshwater crabs. In: Martin, J.W., Crandall, K.A., Felder, D.L. (Eds.), Crustacean Issues 18: Decapod Crustacean Phylogenetics, pp. 491–508.
Cumberlidge, N., Ng, P.K.L., Yeo, D.C.J., Magalhães, C., Campos, M.R., Alvarez, F., ... Ram, M., 2009. Freshwater crabs and the biodiversity crisis: importance, threats, status, and conservation challenges. Biol. Conserv. 142, 1665–1673.
Dai, A.Y., 1999. Fauna Sinica (Arthropoda, Crustacea, Malacostraca, Decapoda, Parathelphusidae, Potamidae). Editorial Committee of Fauna Sinica, Academia Sinica, Science Press, Beijing, pp. 501.
Danielson, J.J., Gesch, D.B., 2011. Global multi-resolution terrain elevation data 2010 (GMTED2010): U.S. Geological Survey Open-File Report 2011. U.S. Geological Survey, Virginia, USA.
Dobson, M.K., 2004. Freshwater crabs in Africa. In: Freshwater Forum. 21. pp. 3–26.
Dobson, M.K., Magana, A.M., Lancaster, J., Mathooko, J.M., 2007. Aseasonality in the abundance and life history of an ecologically dominant freshwater crab in the Rift Valley, Kenya. Freshw. Biol. 52, 215–225.
Dudgeon, D., Cheung, C.P.S., 1990. Selection of gastropod prey by a tropical freshwater crab. J. Zool. 210, 147–155.
Esser, L., Cumberlidge, N., 2008a. *Terrathelphusa kuchingensis*. The IUCN Red List of Threatened Species 2008. e.T134199A3918266.
Esser, L., Cumberlidge, N., 2008b. *Sundathelphusa rubra*. The IUCN Red List of Threatened Species 2008. e.T135109A4058838.
Feria, T.P., Faulkes, Z., 2011. Forecasting the distribution of Marmorkrebs, a parthenogenetic crayfish with high invasive potential, in Madagascar, Europe, and North America. Aquat. Invasions 6, 55–67.
Finkers, J., 1986. Los Yanomami y su sistema alimenticio (Yanomami Nii Pe). Vicariato Apostó´lico de Puerto Ayacucho, Puerto Ayacucho. Monografia n° 2pp. 262.
Foster, J., Harper, D., 2007. Status and ecosystem interactions of the invasive Louisianan red swamp crayfish *Procambarus clarkii* in East Africa. In: Gherardi, F. (Ed.), Biological Invaders in Inland Waters: Profiles, Distribution, and Threats. Springer, pp. 91–101.
Fourcade, Y., Engler, J.O., Rödder, D., Secondi, J., 2014. Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. PLoS One 9, e97122.
France, R., 1992. The North American latitudinal gradient in species richness and geographic range of freshwater crayfish and amphipods. Am. Nat. 139, 342–354.
Freitag, H., 2012. Revision of the genus *Insulamon* Ng & Takeda, 1992 (Crustacea: Decapoda: Potamidae) with description of four new species. Raffles Bull. Zool. 60, 37–55.
García-Guerrero, M., Villarreal, H., Racotta, I., 2003. Effect of temperature on lipids, proteins, and carbohydrates levels during development from egg extrusion to juvenile stage of *Cherax quadricarinatus* (Decapoda: Parastacidae). Comp. Biochem. Physiol. A 135, 147–154.
Gherardi, F., 2007. Understanding the impact of invasive crayfish. In: Gherardi, F. (Ed.), Biological Invaders in Inland Waters: Profiles, Distribution, and Threats. Springer, The Netherlands, pp. 507–542.
Gherardi, F., Cioni, A., 2004. Agonism and interference competition in freshwater decapods. Behavior 141, 1297–1324.
Giam, X., Ng, T.H., Lok, A.F.S.L., Ng, H.H., 2011. Local geographic range predicts freshwater fish extinctions in Singapore. J. Appl. Ecol. 48, 356–363.
Gutiérrez, A.T., Reaser, J.K., 2005. Linkages between Development Assistance and Invasive Alien Species in Freshwater Systems of Southeast Asia. USAID Asia and Near East Bureau, Washington DC, USA, pp. 87.
Hellmann, J.J., Byer, J.E., Bierwagen, B.G., Dukes, J.S., 2008. Five potential consequences of climate change for invasive species. Conserv. Biol. 22, 534–543.
Hentonnen, P., Huner, J.V., 1999. The introduction of alien species of crayfish in Europe. An introduction. In: Gherardi, F., Holdich, D.M. (Eds.), Crayfish in Europe as Alien Species. How to Make the Best of a Bad Situation? AA Balkema, The Netherlands, pp. 13–22.
Hernandez, P.A., Graham, C.H., Master, L.L., Albert, D.L., 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography 29, 773–785.
Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978.
Hobbs, H.H.I.I.I., Jass, J.P., Huner, J.V., 1989. A review of global crayfish introductions with particular emphasis on two North American species (Decapoda, Cambaridae). Crustaceana 56, 299–316.
IPCC, Van der Linden, P.J., 2007. Summary for policymakers. In: Parry, M.L., Canziani, O.F., Palutikof, J.P., Hanson, C.E. (Eds.), Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp. 81–82.
IPCC, 2013. Summary for policymakers. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Midgley, P.M. (Eds.), Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp. 3–29.
Jones, J.P.G., Rasamy, J.R., Harvey, A., Toon, A., Oidtmann, B., Randrianarison, M.H., Raminosoa, N., Ravoahangimalala, O.R., 2009. The perfect invader: a parthenogenic crayfish poses a new threat to Madagascar's freshwater biodiversity. Biol. Invasions 11, 1475–1482.
Kasai, H., Naruse, T., 2003. Potamidae. In: Nishida, M., Shikatani, N., Shokita, S. (Eds.), The Flora and Fauna of Inland Waters in the Ryukyu Islands. Tokai University Press, Tokyo, pp. 282–288 (in Japanese).
Kawai, T., Scholtz, G., Morioka, S., Ramanamandimby, F., Lukhaup, C., Hanamura, Y., 2009. Parthenogenetic alien crayfish (Decapoda: Cambaridae) spreading in Madagascar. J. Crustac. Biol. 29, 562–567.
King, C.R., 1994. Growth and survival of redclaw crayfish hatchlings (*Cherax quadricarinatus* Von Martens) in relation to temperature, with comments on the relative suitability of *Cherax quadricarinatus* and *Cherax destructor* for culture in Queensland. Aquaculture (Netherlands) 122, 75–80.
Larson, E.R., Olden, J.D., 2010. Latent extinction and invasion risk of crayfishes in the southeastern United States. Conserv. Biol. 24, 1099–1110.
Larson, E.R., Renshaw, M.A., Gantz, C.A., Umek, J., Chandra, S., Lodge, D.M., Egan, S.P., 2017. Environmental DNA (eDNA) detects the invasive crayfishes *Orconectes rusticus* and *Pacifastacus leniusculus* in large lakes of North America. Hydrobiologia 800, 173–185.
Leung, B., Lodge, D.M., Finnoff, D., Shogren, J.F., Lewis, M.A., Lamberti, G., 2002. An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. Proc. R. Soc. B 269, 2407–2413.
Lodge, D.M., Stein, R.A., Brown, K.M., Covich, A.P., Bronmark, C., Garvey, J.E., Klosiewski, S.P., 1998. Predicting impact of freshwater exotic species on native biodiversity: challenges in spatial scaling. Aust. J. Ecol. 23, 53–67.
Lodge, D.M., Deines, A., Gherardi, F., Yeo, D.C.J., Arcella, T., Baldridge, A.K., ... Zeng, Y., 2012. Global introductions of crayfishes: evaluating the impact of species invasions on ecosystem services. Annu. Rev. Ecol. Evol. Syst. 43, 449–472.
Lodge, D.M., Simonin, P.W., Burgiel, S.W., Keller, R.P., Bossenbroek, J.M., Jerde, C.L., ... Zhang, H., 2016. Risk analysis and bioeconomics of invasive species to inform policy and management. Annu. Rev. Environ. Resour. 41, 453–488.
Lukhaup, C., 2015. Cherax (Astaconephrops) pulcher, a new species of freshwater crayfish (Crustacea, Decapoda, Parastacidae) from the Kepala Burung (Vogelkop) Peninsula, Irian Jaya (West Papua), Indonesia. ZooKeys 502, 1–10.
Maitland, D.P., 2003. Predation on snakes by the freshwater land crab Eudaniela garmani. J. Crustac. Biol. 23 (1), 241–246.
Meade, M., Doeller, J., Kraus, D., Watts, S.A., 2002. Effects of temperature and salinity on weight gain, oxygen consumption rate, and growth efficiency in juvenile red-claw crayfish *Cherax quadricarinatus*. J. World Aquacult. Soc. 33, 188–198.
Merow, C., Smith, M.J., Silander Jr., J.A., 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography 36, 1058–1069.
Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M., Anderson, R.P., 2014. ENMeval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for MAXENT ecological niche models. Methods Ecol. Evol. 5, 1198–1205.
Naimi, B., 2015. usdm: Uncertainty analysis for species distribution models. In: R Package Version 1.1-12, . http://CRAN.R-project.org/package=usdm.
Ng, P.K.L., 1988. The Freshwater Crabs of Peninsular Malaysia and Singapore. Department of Zoology, National University of Singapore, Shinglee Press, Singapore, pp. 156.
Ng, P.K.L., 1989. *Terrathelphusa*, a new genus of semiterrestrial freshwater crabs from Borneo and Java (Crustacea: Decapoda: Brachyura: Sundathelphusidae). Raffles Bull. Zool. 37, 116–131.
Ng, P.K.L., Yeo, D.C.J., 2007. Malaysian freshwater crabs: conservation prospects and challenges. In: Chua, L. (Ed.), Proceedings of the Seminar on the Status of Biological Diversity in Malaysia and Threat Assessment of Plant Species in Malaysia, 28–30 June 2005. Forest Research Institute Malaysia, Kepong, pp. 95–120.
Ng, D.J.J., Yeo, D.C.J., Sivasothi, N., Ng, P.K.L., 2014. Conservation challenges and action for the critically endangered Singapore freshwater crab *Johora singaporensis*. Oryx 49, 345–351.
Ng, D.J.J., McGowan, P.J.K., Raghavan, R., Cai, Y., Cumberlidge, N., Davison, G., ... Yeo, D.C.J., 2015. Conservation Strategy for the Singapore Freshwater Crab Johora singaporensis. https://www.nparks.gov.sg/~/media/nparks-real-content/biodiversity/programmes-and-initiatives/conservation_strategy_johora.pdf?la=en, Accessed date: 30 April 2018 Singapore.
Nghiem, L.T.P., Soliman, T., Yeo, D.C.J., Tan, H.T.W., Evans, T.A., Mumford, J.D., ... Carrasco, L.R., 2013. Economic and environmental impacts of harmful non-indigenous species in Southeast Asia. PLoS One 8, e71255.
Ogada, M.O., 2006. Effects of the Louisiana Crayfish Invasion and Other Human Impacts on the African Clawless Otter (Ph.D. Thesis). Kenyatta University, Kenya.
Olden, J.D., Vander Zanden, M.J., Johnson, P.T.J., 2011. Assessing ecosystem vulnerability to invasive rusty crayfish (*Orconectes rusticus*). Ecol. Appl. 21, 2587–2599.
Patoka, J., Wardiatno, Y., Yonvitner, Kuříková, P., Petrtýl, M., Kalous, L., 2016. *Cherax quadricarinatus* (von Martens) has invaded Indonesian territory west of the Wallace line: evidences from Java. Knowl. Manag. Aquat. Ecosyst. 417, 1–6.
Pearson, R.G., Raxworthy, C.J., Nakamura, M., Peterson, A.T., 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J. Biogeogr. 34, 102–117.
Peh, K.S.-H., 2010. Invasive species in Southeast Asia: the knowledge so far. Biodivers. Conserv. 19, 1083–1099.
Pethiyagoda, R., 1994. Threats to the indigenous freshwater fishes of Sri Lanka and remarks on their conservation. Hydrobiologia 285, 189–201.
Phillips, S.J., 2008. Transferability, sample selection bias and background data in presence-only modelling: a response to Peterson et al. (2007). Ecography 31, 272–278.
Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190, 231–259.

Poesch, M.S., Chavarie, L., Chu, C., Pandit, S.N., Tonn, W., 2016. Climate change impacts on freshwater fishes: a Canadian perspective. Fisheries 41, 385–391.
Pretzmann, G., 1987. A contribution to a historic analysis of Mediterranean freshwater decapods chorology. Investig. Pesq. 51, 17–25.
Purvis, A., Gittleman, J.L., Cowlishaw, G., Mace, G.M., 2010. Predicting extinction risk in declining species. Proc. R. Soc. B 267, 1947–1952.
R Development Core Team, 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, URL. http://www.R-project.org/ (accessed 02.07.17).
Reynolds, J.D., Souty-Grosset, C., Richardson, A.M.M., 2013. Ecological roles of crayfish in freshwater and terrestrial habitats. Freshwater Crayfish 19, 197–218.
Rhoden, C.M., Peterman, W.E., Taylor, C.A., 2017. Maxent-directed field surveys identify new populations of narrowly endemic habitat specialists. PeerJ 5, e3632.
Rodda, G.H., Jarnevich, C.S., Reed, R.N., 2011. Challenges in identifying sites climatically matched to the native ranges of animal invaders. PLoS One 6, e14670.
Rödder, D., Engler, J.O., 2011. Quantitative metrics of overlaps in Grinnellian niches: advances and possible drawbacks. Glob. Ecol. Biogeogr. 20, 915–927.
Rosenthal, S.K., Stevens, S.S., Lodge, D.M., 2006. Whole-lake effects of invasive crayfish (*Orconectes* spp.) and the potential for restoration. Can. J. Fish. Aquat. Sci. 63, 1276–1285.
Sala, O.E., Chapin, F.S.I.I.I., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., ... Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. Science 287, 1770–1774.
Savvides, P., Louca, V., Sfenthourakis, S., 2015. Competition for shelter occupancy between a native freshwater crab and an invasive crayfish. Aquat. Ecol. 49, 273–278.
Schoener, T.W., 1968. The Anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology 49, 704–726.
Schrimpf, A., Chucholl, C., Schmidt, T., Schulz, R., 2013. Crayfish plague agent detected in populations of the invasive North American crayfish *Orconectes immunis* (Hagen, 1870) in the Rhine River, Germany. Aquat. Invasions 8, 103–109.
Seitz, R., Vilpoux, K., Hopp, U., Harzsch, S., Maier, G., 2005. Ontogeny of the Marmorkrebs (marbled crayfish): a parthenogenetic crayfish with unknown origin and phylogenetic position. J. Exp. Zool. 303, 393–405.
Shcheglovitova, M., Anderson, R.P., 2013. Estimating optimal complexity for ecological niche models: a jackknife approach for species with small sample sizes. Ecol. Model. 269, 9–17.
Soberón, J., 2007. Grinnellian and Eltonian niches and geographic distributions of species. Ecol. Lett. 10, 1115–1123.
Sodhi, N.S., Koh, L.P., Brook, B., Ng, P.K.L., 2004. Southeast Asian biodiversity: an impending disaster. Trends Ecol. Evol. 19, 654–660.
Sodhi, N.S., Bickford, D., Diesmos, A.C., Tien Ming, L., Lian, P.K., Brook, B.W., Sekercioglu, C.H., Bradshaw, C.J.A., 2008. Measuring the meltdown: drivers of global amphibian extinction and decline. PLoS One 3 (2), e1636.
Sodhi, N.S., Koh, L.P., Clements, R., 2010. Conserving Southeast Asian forest biodiversity in human-modified landscapes. Biol. Conserv. 143, 2375–2384.
Stahl, M.O., Tarek, M.H., Yeo, D.C.J., Badruzzaman, A.B.M., Harvey, C.F., 2014. Crab burrows as conduits for groundwater-surface water exchange in Bangladesh. Geophys. Res. Lett. 41, 8342–8347.
Svoboda, J., Strand, D.A., Vrålstad, T., Grandjean, F., Edsman, L., Kozák, P., ... Petrusek, A., 2014. The crayfish plague pathogen can infect freshwater-inhabiting crabs. Freshw. Biol. 59, 918–929.
Thomas, C.D., Cameron, A., Green, R.E., 2004. Extinction risk from climate change. Nature 427, 145–148.
Tsang, L.M., Schubart, C.D., Ahyong, S.T., Lai, J.C.J., Au, E.Y.C., Chan, T.-Y., Ng, P.K.L., Chu, K.H., 2014. Evolutionary history of true crabs (Crustacea: Decapoda: Brachyura) and the origin of freshwater crabs. Mol. Biol. Evol. 31, 1172–1187.
Uchida, H., Nelson, A., 2009. Agglomeration index: towards a new measure of urban concentration. In: Beall, J., Guha-Khasnobis, B., Kanbur, R. (Eds.), Urbanization and Development. Multidisciplinary Perspectives. Oxford University Press, UK, pp. 1–18.
Vogt, G., 2015. Bimodal annual reproduction pattern in laboratory-reared marbled crayfish. Invertebr. Reprod. Dev. 59, 218–223.
Wanjit, C., Chaichana, R., 2013. In: Some biology and ecological risk assessment of crayfish on freshwater resources and establishment of crayfish in Pra Pong Reservoir, Sra Keaow province. Proceedings: International Graduate Research Conference. pp. 161–166.
Warren, D.L., Glor, R.E., Turelli, M., 2010. ENMTools: a toolbox for comparative studies of environmental niche models. Ecography 33, 607–611.
Wenger, S.J., Olden, J.D., 2012. Assessing transferability of ecological models: an underappreciated aspect of statistical validation. Methods Ecol. Evol. 3, 260–267.
Wisz, M.S., Hijmans, R.J., Peterson, A.T., Graham, C.H., Guisan, A., CEAS Predicting Species Distributions Working Group, 2008. Effects of sample size on the performance of species distribution models. Divers. Distrib. 14, 763–773.
Wizen, G., Galil, B.S., Shlagman, A., Gasith, A., 2008. First record of red swamp crayfish, *Procambarus clarkii* (Girard, 1852) (Crustacea: Decapoda: Cambaridae) in Israel—too late to eradicate? Aquat. Invasions 3, 181–185.
Woodruff, D.S., 2010. Biogeography and conservation in Southeast Asia: how 2.7 million years of repeated environmental fluctuations affect today's patterns and the future of the remaining refugial-phase biodiversity. Biodivers. Conserv. 19, 919–941.
Woodward, G., Perkins, D.M., Brown, L.E., 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. Philos. Trans. R. Soc. B 365, 2093–2106.
Yeo, D.C.J., Ng, P.K.L., 1998. Freshwater crabs of the *Potamon tannanti* species group (Crustacea, Decapoda, Brachyura, Potamidae) of northern Indochina. Raffles Bull. Zool. 46, 627–650.
Yeo, D.C.J., Ng, P.K.L., Cumberlidge, N., Magalhães, C., Daniels, S.R., Campos, M.R., 2008. A global assessment of freshwater crab diversity (Crustacea: Decapoda: Brachyura). In: Balian, E.V., Lévequè, C., Segers, H., Martens, M. (Eds.), Freshwater Animal Diversity Assessment. Hydrobiologia. 595. pp. 275–286.
Yeo, D.C.J., Cumberlidge, N., Klaus, S., 2014. Preface—freshwater decapod biology in the 21st century. In: Yeo, D.C.J., Cumberlidge, N., Klaus, S. (Eds.), Advances in Freshwater Decapod Systematics and Biology. Crustaceana Monographs. 19. pp. 1–6.
Yeo, D.C.J., Luz, S., Cai, Y., Cumberlidge, N., McGowan, P.J.K., Ng, D.J.J., Raghavan, R., Davison, G.W.H., 2016. Conservation first: Strategic planning to save the Critically Endangered Singapore freshwater crab, *Johora singaporensis*. In: Kawai, T., Cumberlidge, N. (Eds.), A Global Overview of the Conservation of Freshwater Decapod Crustaceans. Springer International Publishing, pp. 359–372.
Zeng, Y., 2017. Natural and Human-Mediated Interactions between Freshwater Crabs and Crayfish (Unpublished Ph.D. Thesis). National University of Singapore, Singapore.
Zeng, Y., Chong, K.W., Grey, E.K., Lodge, D.M., Yeo, D.C.J., 2015. Disregarding human pre-introduction selection can confound invasive crayfish risk assessments. Biol. Invasions 17, 2373–2385.
Zeng, Y., Low, B.W., Yeo, D.C.J., 2016. Novel methods to select environmental variables in MaxEnt: a case study using invasive crayfish. Ecol. Model. 341, 5–13.